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**The potential for indirect negative effects of exotic insect species on a liverwort, *Bazzania trilobata* (Lepidoziaceae), mediated by the decline of a foundation tree species, *Tsuga canadensis* (Pinaceae)<sup>1</sup>**

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# The potential for indirect negative effects of exotic insect species on a liverwort, *Bazzania trilobata* (Lepidoziaceae), mediated by the decline of a foundation tree species, *Tsuga canadensis* (Pinaceae)<sup>1</sup>

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**Abstract.** In many ecological communities, the effects of exotic species are likely to extend beyond their direct interactions with natives, due to indirect effects. This dynamic might be particularly consequential in cases where invasive insects or other exotic herbivores target foundation plant species in the communities they invade. In this study at a site in western Massachusetts, we used experimental transplants to gauge the potential effects of a decline in the evergreen conifer *Tsuga canadensis* due to ongoing spread of two exotic insect pests on a liverwort, *Bazzania trilobata*, whose distribution is closely linked to dense stands of this conifer in the northeastern USA. After 4 years, transplanted *B. trilobata* samples moved to forest areas with lower abundance of *T. canadensis* declined significantly, particularly on sites with higher solar radiation, as determined by local slope and aspect. In addition, samples manually cleared of deciduous leaf litter were ~ 17% larger than those exposed to natural accumulation of leaf litter, indicating a direct negative effect of deciduous trees on the liverwort that might increase as these tree species replace *T. canadensis* lost to invasive pests. A parallel experiment documented high mortality of *B. trilobata* (55%) when subjected to open canopy conditions similar to those resulting from selective “salvage” logging of hemlock in the region. These results indicate that the spread of exotic insect pests targeting *T. canadensis* is likely to produce strong indirect negative effects on the liverwort *B. trilobata*, via diminished commensal interactions with the conifer and increased amensalistic effects from the deciduous tree species that commonly replace it.

Key words: amensalism, commensalism, elongate hemlock scale, exotic species, hemlock woolly adelgid, invasions, liverwort

Indirect ecological effects associated with the spread of exotic invasive species have been documented with increasing frequency in recent years (Stinson *et al.* 2006, Kenis *et al.* 2009, Rodriguez-Cabal *et al.* 2013, Waser *et al.* 2015). Under these ecological circumstances, direct interactions between, for example, an exotic insect and its native host plant species, also have detectable negative effects on other species in an ecosystem (White *et al.* 2006). This dynamic can be especially disruptive if the native species targeted by exotics is also an abundant “foundation species” in its ecosystem, creating distinctive

environmental conditions that support a unique assemblage of other native species (Ellison *et al.* 2005, Lovett *et al.* 2006).

In the eastern United States, many forest ecosystems are dominated by the evergreen conifer eastern hemlock (*Tsuga canadensis* (L.) Carrière), a tree species that generates distinctive understory environments characterized by cool, low-light conditions and the development of a deep, acidic soil organic layer (Ellison *et al.* 2005, Lovett *et al.* 2006). However, these forest communities have experienced significant decline and dramatic compositional shifts in recent decades due to invasion by two exotic invasive insect pests: the hemlock woolly adelgid (*Adelges tsugae* Annand; hereafter HWA) and the elongate hemlock scale (*Fiorinia externa* Ferris; hereafter EHS) (Orwig and Foster 1998, Ellison *et al.* 2005). Invasive HWA is an aphid-like insect native to *Tsuga* species in Japan that was first detected on USA native *T. canadensis* in Virginia around 1950 (Souto *et al.* 1996, Havill *et al.* 2006, Preisser *et al.* 2011). It has since dramatically expanded its range in the eastern USA, including invasion of southern and central New England, where HWA has had a well-documented presence on *T. canadensis* since 1985 (McClure 1990, Orwig *et al.* 2002). Elongate hemlock scale also originated on *Tsuga* species in

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eastern Asia, and was first observed infesting *T. canadensis* in New York City in 1908 (Sasscer 1912, Preisser *et al.* 2011). Significant damage to *T. canadensis* occurs when these insects attach to needles or small stems and consume either parenchyma (in the case of HWA) or mesophyll tissue (EHS). Large populations of these pests on *T. canadensis* lead to needle loss, canopy thinning, and, eventually, tree decline or death (Young *et al.* 1995, McClure 2002, Preisser *et al.* 2011).

The regional decline of *T. canadensis* associated with HWA and EHS invasion has had significant effects on forest ecosystem processes and associated ecological communities (Jenkins *et al.* 1999, Ellison *et al.* 2005, Zuskwert *et al.* 2014). To date, the importance of the distinctive environmental conditions created by *T. canadensis* for other species has been established primarily through studies of terrestrial and aquatic fauna, including eastern red-backed salamanders (*Plethodon cinereus* Green) (Mathewson 2009), black-throated green warblers (*Dendroica virens* Gmelin) (Tingley *et al.* 2002), macroinvertebrates (Snyder *et al.* 2002), forest floor mesofauna (Zuskwert *et al.* 2014), and fish (Ross *et al.* 2003, Ellison *et al.* 2005). In contrast, the understory environment of dense *T. canadensis* forests appears to be relatively inhospitable to most vascular plant species, likely due to low light levels and limited nutrient availability. This tends to result in low vascular plant diversity, as well as a lack of vascular plant species that have been clearly identified as being dependent on *T. canadensis* as a foundation species (Thompson and Sorenson 2000, Eschtruth *et al.* 2006, D'Amato *et al.* 2009, Ellison *et al.* 2016). The one notable exception to this pattern might be seen among nonvascular plants, where several moss and liverwort species are typically found inhabiting *T. canadensis* stands (Cleavitt *et al.* 2008) and bryophyte cover tends to be high.

The small stature and poikilohydric nature of bryophytes might contribute to their positive association with *T. canadensis* forests: competition from larger-statured vascular plants in the understory is likely reduced, the potential for burial by coarse-textured deciduous leaf litter is lessened, and water stress might be decreased. In these types of conifer-dominated ecosystems, bryophytes appear to take on an outsized role in nutrient cycling and other environmental processes, such as is seen in boreal forests (Bonan and Shugart 1989, Jean *et al.* 2017), implying that some ecosystem changes

seen with shifts from conifer- to deciduous-dominated canopies could be influenced by disruption of the bryophyte-dominated forest floor community. Overall, if *T. canadensis*-dependent plant species do exist, it seems most probable that they would be found among the relatively understudied bryophyte flora of these forest ecosystems. Further, it would be among these diminutive, nonvascular plant species that indirect negative effects of the exotic pests HWA and EHS might be most likely as *T. canadensis* declines. These ecological dynamics could be further exacerbated by direct human actions, as the impending loss of *T. canadensis* has led many foresters and land managers to preemptively cut stands of the tree species to salvage some economic value from the lumber (Orwig *et al.* 2002, 2012; Lustenhouwer *et al.* 2012).

Among forest understory bryophytes commonly observed in *T. canadensis* forests in the northeastern USA, the liverwort *Bazzania trilobata* (L.) Gray is notable for often being particularly abundant and forming extensive mats in mature stands on mesic sites. This bryophyte species has been the focus of some prior research related to forest disturbance; for example, Sollows *et al.* (2001) investigated the survival of *B. trilobata* under clear-cut conditions in New Brunswick, Canada, and under simulated stress conditions in the laboratory. They found that while samples of *B. trilobata* were sensitive to desiccation in the lab, its dense colonial mat growth form appeared to permit survival, at least temporarily, under open canopy conditions in the field in Canada. Farther south, in New Hampshire, Cleavitt *et al.* (2007) conducted an experiment to evaluate the effects of water availability and nutrient additions on *B. trilobata* growth. Their results indicated that a complex balance among water, nutrient, and light availability was necessary for maintaining positive carbon gain in the species, suggesting a high sensitivity to understory environmental conditions (Cleavitt *et al.* 2007). As *B. trilobata* is most commonly found in high abundance under *T. canadensis* canopies in southern and central New England, it appears that its ecophysiological characteristics and ecological niche requirements are best matched by environmental conditions found in forests dominated by this foundation tree species.

In this study, we used multi-year experimental transplants of *B. trilobata* to investigate the

potential effects of the impending *T. canadensis* decline on the liverwort's survival and performance. To do this we translocated *B. trilobata* gametophyte mat samples to forest sites with varying abundance of *T. canadensis* across a range of topographic settings (e.g., variation in slope, aspect, soil moisture) at a study site in western Massachusetts where *T. canadensis* forests are still intact. This approach incorporated aspects of a space-for-time substitution experiment, mimicking different stages of hemlock loss from the canopy and its replacement by broad-leaved deciduous trees (e.g., black birch, *Betula lenta* L.), as has been seen in areas to the south (e.g., Orwig and Foster 1998), and should provide insight into the stresses *B. trilobata* might experience in the future with complete *T. canadensis* decline due to exotic insects or salvage logging. Similar space-for-time comparisons and experiments have been used to study ecosystem changes expected with *T. canadensis* decline elsewhere in New England (Orwig *et al.* 2013), using present-day deciduous forests near *T. canadensis* stands as proxies for the forests that are likely to replace the declining conifer. Importantly, undertaking the research now, prior to loss of *T. canadensis* from the area, allowed for control treatments in healthy *T. canadensis* forests: a significant point of comparison for experimental sites with lower *T. canadensis* abundance (cf. Orwig *et al.* 2013). Such comparisons would not be possible in a more traditional longitudinal study that tracked *B. trilobata* experiencing actual pest-induced *T. canadensis* decline in the region, and the time necessary to later evaluate *B. trilobata* performance in the deciduous forests that typically develop in the wake of *T. canadensis* loss would require many more years.

Within the experimental space-for-time substitution framework used in our study, we investigated three key research questions: (a) How does the survival and performance of *B. trilobata* relate to abiotic factors and the structure and tree species composition of forest stands, including potential positive effects of *T. canadensis* that could be diminished with the tree species' decline? (b) Will the predicted increase in deciduous tree species following *T. canadensis* decline exert further negative effects on *B. trilobata* via deciduous leaf litter burial? (c) Are common forest management practices used in response to *T. canadensis* decline, such as preemptive salvage logging, compatible with survival of *B. trilobata*?

**Materials and Methods.** **STUDY SPECIES.** *Bazzania trilobata* is a leafy liverwort with a circum-boreal distribution in forests of western Europe, portions of the eastern and western USA, and Japan (Fig. 1A–C; Schuster 1969, Buczkowska *et al.* 2010). The gametophyte life stage is characterized by distinctive trilobed and dentate leaves with a pattern of incubus leaf insertion (Crum 1991, Lincoln 2008, Damsholt and Pugh 2009). The species is dioecious, with separate male and female gametophyte plants; sporophytes are only rarely produced (Fig. 1B; Schuster 1969, Lincoln 2008, Damsholt and Pugh 2009). In appropriate habitats in the eastern USA, *B. trilobata* forms extensive gametophyte mats on moist soil, rocks, and well-rotted coarse woody debris, underscoring the species' apparent reliance on vegetative spread rather than sexual reproduction (Fig. 1C). There is also evidence that the extensive gametophyte mats seen in many populations likely comprise single, long-lived clones, further limiting possibilities for sexual reproduction (Schuster 1969, Cleavitt *et al.* 2007).

Across its geographic range, *B. trilobata* is typically associated with shady and moist forest understory environments, conditions that stands of evergreen coniferous trees often provide (Buczkowska *et al.* 2010). The species has been reported as averse to calcareous soils and has typically been observed colonizing acidic rock types and substrates (Crum 1991). Consistent with these preferences, *B. trilobata* often inhabits *T. canadensis* forests in the northeastern USA (Cleavitt *et al.* 2007), an ecosystem noted for its cool, moist, acidic understory conditions (Ellison *et al.* 2005). The species has also been reported from *Thuja occidentalis* L. swamps in the midwestern USA, and old growth *Picea abies* (L.) H. Karst forests in Poland (Crum 1991, Buczkowska *et al.* 2010).

**STUDY SITE AND GRADIENT TRANSPLANT EXPERIMENT.** The study site for this research was located at Smith College's Ada and Archibald MacLeish Field Station and adjacent forest areas in Conway and Whately, MA (42°27.32'N, 72°40.96'W). The region lies within the Northern Hardwoods–Hemlock–White Pine forest type of New England (Westveld 1956), and *B. trilobata* can be found as an abundant ground layer species in many mature *T. canadensis* forests in the area. To better understand the ecological niche of *B. trilobata* and gauge the species' likely response to changing environmental conditions that might be triggered

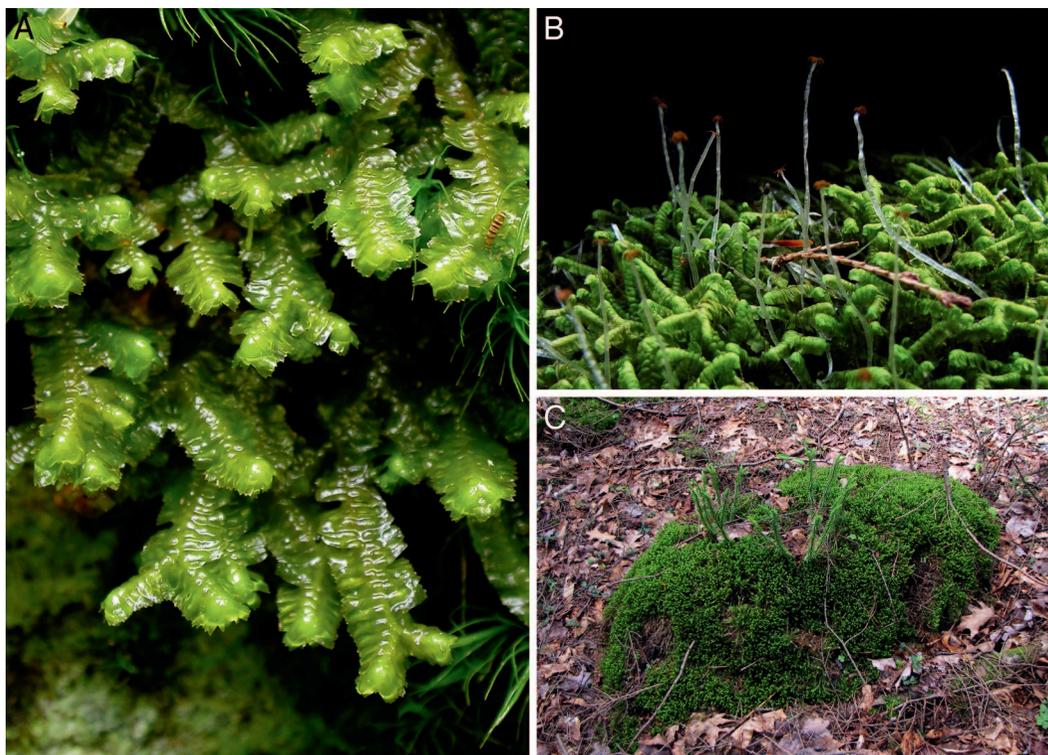


FIG. 1. *Bazzania trilobata* is a leafy liverwort commonly seen in mesic *Tsuga canadensis*-dominated forests in New England. (A) The gametophyte exhibits incubus leaf insertion and trilobed, dentate leaves. (B) Sporophytes are nonphotosynthetic, ephemeral, and emerge from female gametophytes; however, they are rarely observed. (C) Clonal gametophyte mats of *B. trilobata* typically spread vegetatively on the forest floor and over rocks and coarse woody debris. Note: *Huperzia lucidula* (Michx.) Trevisan at center of *B. trilobata* mat in C is ~ 15 cm tall.

by decline of *T. canadensis* forests, a multi-year experimental transplant study was conducted to expose *B. trilobata* to varying forest composition and understory environments.

In June 2013, gametophyte mat samples of *B. trilobata* were collected from a mature *T. canadensis* forest in Conway, MA, and subdivided and randomized into 172 circular experimental units (~ 10 cm in diameter). As a control, 20 of these samples were reinstalled into this source site along a 50-m transect where *B. trilobata* occurred naturally. The remaining 152 samples were moved to a nearby forest area at the MacLeish Field Station (~ 200–300 m distant) and placed along a series of seven 50–100-m transects traversing environmental gradients of varying canopy tree species composition (e.g., evergreen *T. canadensis* vs. deciduous species), tree stem density, and underlying abiotic conditions. Six of these transects were oriented south-to-north, and traversed portions of the steep, north-facing slope of an

ephemeral stream valley, as well as the opposite south-facing slope. Five of these transects extended 10–20 m into a recently logged forest with lower tree density and more open canopy conditions on the north edge of the experimental site. The seventh transect ran west-to-east on level ground parallel to the ephemeral stream channel on mesic to hydric soils.

The gametophyte samples at the control and experimental sites were installed as a series of pairs (set 1 m apart within pairs) along each transect, with 5-m spacing between adjacent pairs along the transects. Each sample was placed on a uniform substrate of well-rotted *T. canadensis* wood collected from large coarse woody debris elements on the forest floor at the control site. The rotted wood material was pooled, broken up, and mixed by hand until it formed a homogenous mixture with a loose, crumbly texture. At each sample point, loose leaf litter was cleared and a ~ 300–400-mL volume of rotted wood was installed

as a small mound. The *B. trilobata* specimens were then positioned on this uniform substrate and anchored in place by a layer of black plastic deer-fence netting secured to the ground with landscape staples. For half of the samples (one per pair), subsequent deciduous leaf litter fall was actively cleared from the samples over the course of the experiment to avoid burial of the low-statured gametophytes; the other sample in each pair was allowed to naturally accumulate leaf litter over the course of the study.

From July 2013 until June 2017 the samples were monitored during the growing season and any accumulated deciduous leaf litter was cleared from half of the samples. Sample status (stable vs. declining or dead) was documented during repeated surveys (e.g., Jackson 2015) and a final survey was conducted in June 2017. For the 2016–17 surveys, change in sample size was estimated as a percentage of value of the original 10-cm-diameter sample units using a gridded clear plastic sheet placed over each sample. Samples were visually scored on a scale from 0% (dead), 1–5% of original specimen area alive, 5–10%, 10–20%, and upwards in 10% intervals, including a 100–110% category for samples that grew beyond their original dimensions. The final June 2017 size percentage estimates were used in the multiple linear regression analyses described below.

To explore how varying abiotic and biotic conditions affected *B. trilobata* survival and growth, several environmental factors hypothesized to be important for forest bryophytes were quantified at each sample point along the transects. Forest floor moisture levels were estimated by measuring surface soil moisture content (%): Organic layer soil samples were collected on June 24, 2014, after a 1-wk+ period without rainfall from 25 × 25-cm quadrats positioned adjacent to the experimental *B. trilobata* samples. The fresh, field-moist weight of each soil sample was determined, followed by 48 hr in drying ovens at 70 °C to determine oven-dry soil mass and to estimate original soil moisture content. Incoming solar radiation or insolation (MJ/m<sup>2</sup> per day) was also estimated for each point based on local slope and aspect using the climate model ClimCalc (Ollinger *et al.* 1995, 2001) to obtain monthly solar radiation estimates. To test for the effects of local tree species composition and abundance on *B. trilobata* samples, a forestry angle gauge was used to tally all tree stems that exceeded a basal area

factor of 5 around each point. Although this approach did not involve surveying fixed area plots at each point, it should provide a more biologically meaningful estimate of the individual trees that directly influence the localized understory environment around each sample point (*i.e.*, large-diameter trees farther away are included in the tally, while smaller-diameter trees are only included if closer to the sample point). Forest structure variables quantified included total number of trees per sample point, total number of *T. canadensis* per point, and proportion of *T. canadensis* trees per point.

**CLEAR-CUT VS. INTACT FOREST TRANSPLANT EXPERIMENT.** In July 2014, a second transplant experiment was initiated to more directly test the effects of clear-cut conditions on *B. trilobata* survival and performance, as preemptive “salvage logging” has been a common management response to the spread of the exotic insect pests affecting *T. canadensis*. In an area at the MacLeish Field Station adjacent (~ 100 m west) to that used in the gradient transplant experiment described above, two sets of 20 individual *B. trilobata* mat samples were installed in a pair of 20 × 25-m plots using a 5 × 5-m spacing grid for samples within plots. Following the procedure of the initial transplant experiment described above, the samples of *B. trilobata* were positioned on a substrate of rotted *T. canadensis* wood and anchored with deer-fence netting. One plot was established in an open area cleared by intensive logging in 2005–06 when most of the *T. canadensis* forest canopy was removed. The second plot was established in an intact forest area ~ 50 m to the south of the clear-cut plot under a well-developed forest canopy of *T. canadensis* and deciduous trees. The size and status of these *B. trilobata* samples (alive vs. dead) was tracked during the summer growing season from July 2014 until a final survey in June 2017 (3 yr).

**DATA ANALYSES.** To explore the relationship between environmental factors and final *B. trilobata* size along the experimental and control transects, a subset of the environmental predictors measured were combined and analyzed in a multiple linear regression model. A correlation matrix was generated to assess cross-correlations and multicollinearity among the environmental predictor variables, and only those with  $R < 0.80$  were included. Only the subset of *B. trilobata*

samples cleared of deciduous leaf litter were used in the multiple regression analysis in order to more clearly identify environmental effects on performance, separate from the direct effects of leaf litter burial. To evaluate the effect of deciduous leaf litter burial on the performance *B. trilobata*, the paired samples with and without leaf litter removal were analyzed with a paired samples (Student's) *t* test. For the second transplant experiment evaluating the effects of clear-cut conditions on *B. trilobata* survival, a Pearson's  $\chi^2$  test with a Yates' continuity correction was used to compare the status (alive vs. dead in June 2017) of *B. trilobata* specimens in the clear-cut vs. intact forest plots. All analyses were conducted in RStudio Version 1.0.136 (RStudio Team 2015).

**Results.** PERFORMANCE OF TRANSPLANTED *B. TRILOBATA* ALONG ENVIRONMENTAL GRADIENTS. All the *B. trilobata* samples collected and replanted at the control site (*i.e.*, source site) survived the process of collection, division, and replanting in Year 1 of the experiment (2013). However, two samples at this location were eventually lost due to animal disturbance in Year 3. On average, the 18 intact control site specimens were  $65.4\% \pm 8.5\%$  SE of their original size (circular, 10-cm diameter) at the conclusion of the experiment in June 2017. Mortality was low, with only 1 of these 18 intact control samples (5.6%) declining and dying over the 4-years monitoring period. Four control samples (constituting 22% of the total number of intact control specimens) were stable or larger in size by the end of the experiment (90–100% or 100–110% size classes), including two that increased in size beyond the original sample size; other samples reestablished but were smaller in size by June 2017. In contrast, *B. trilobata* samples moved to the environmental gradient transects outside the control site experienced higher mortality, and modestly lower growth rates among surviving samples: 27 samples declined and died outright (17.8% mortality) and the mean size of samples after 4 yr was  $34.7\% \pm 2.8\%$  SE of original size. However, nine samples (13.2%) at the experimental site were the same size or slightly larger by the conclusion of the experiment (*i.e.*, size classes 90–100% or 100–110%).

The multiple linear regression used to test the relationship between *B. trilobata* performance (*i.e.*, final size after 4 yr) and environmental factors included four predictors: total trees around each

sample point, the proportion of these trees that were *T. canadensis*, percentage of soil moisture, and solar radiation. These factors varied considerable across the transects and control site: total trees ranged from 6 to 35 ( $21.6 \pm 0.9$  SE); the proportion of tree stems that were *T. canadensis* ranged from 0 to 0.93 ( $0.44 \pm 0.02$  SE). Soil organic layer moisture content values ranged from 33% to 84% ( $59\% \pm 2\%$  SE). Solar radiation, based on slope and aspect, ranged from 9.2 MJ/m<sup>2</sup> per day on the steep north-facing slope, to 16.0 MJ/m<sup>2</sup> per day on the south-facing slope ( $13.5$  MJ/m<sup>2</sup> per day  $\pm 0.1$  MJ/m<sup>2</sup> per day SE). The multiple linear regression model relating *B. trilobata* performance these predictors was highly significant ( $F_{4,80} = 6.96$ ,  $P = 0.00007$ ,  $R^2 = 0.26$ ). Of the four environmental factors, *B. trilobata* performance was found to be significantly correlated ( $P < 0.05$ ) with three: average solar radiation, total trees, and the proportion of *T. canadensis* stems among trees around each sample point; soil moisture was nonsignificant (Table 1). Interaction effects among the environmental factors were also tested, but none were significant ( $P > 0.05$ ) and they were not included in the final model. The performance of *B. trilobata* was most strongly influenced by solar radiation levels ( $P = 0.005$ ), as determined by slope and aspect, with samples dying or declining most substantially at points with higher insolation (*e.g.*, south-facing slopes). Somewhat counterintuitively, performance was negatively associated with the total number of trees around sample points ( $P = 0.0014$ ), a pattern driven by higher performance of *B. trilobata* at sample points under well-developed canopies of mature, widely spaced trees compared to areas with higher density of smaller-diameter trees and lower canopy (*e.g.*, near the area that was recently logged). The performance of *B. trilobata* also exhibited a significant positive association with the proportion of stems around each sample point that were *T. canadensis* ( $P = 0.0486$ ; Table 1).

LEAF LITTER REMOVAL AND *B. TRILOBATA* PERFORMANCE. At each sample point in the control site and along the environmental gradient transects ( $N = 86$ ), two *B. trilobata* specimens were originally installed in July 2013, one of which was actively cleared of deciduous leaf litter during each subsequent growing season. Of these 86 sample pairs, 77 included at least one specimen still alive at the conclusion of the experiment in June 2017 (*i.e.*, both specimens declined and died at eight

Table 1. Results from a multiple linear regression model relating the final percentage of size of *Bazzania trilobata* specimens to environmental predictors. The overall model was highly significant ( $F_{4,80} = 6.96$ ,  $P = 0.00007$ ,  $R^2 = 0.26$ ). Interactions among predictors were also explored, but were not significant and thus were not included in the final model.

Predictor variables	Estimate	SE	<i>t</i> value	<i>P</i> value
Solar radiation	-11.8630	3.2460	-3.6540	0.0005
Total no. of trees	-1.7320	0.5250	-3.3000	0.0014
% <i>Tsuga canadensis</i>	41.5010	20.7020	2.0030	0.0486
% soil moisture	0.2240	0.2790	0.8040	0.4237

sample points, plus one pair was destroyed by animal activity). For these 77 pairs, a statistically significant effect of the leaf litter removal treatment was evident: Samples of *B. trilobata* that were cleared of deciduous leaf litter were, on average,  $16.5\% \pm 5.0\%$  SE larger than adjacent samples that were left uncleared (paired samples Student's *t* test:  $t = -3.3184$ ,  $P = 0.0014$ ). This overall trend included 10 cases where the uncleared sample in a pair declined and died, while the cleared sample survived ( $\sim 13\%$ ), but only 2 cases where the specimen with leaf litter removed died while the uncleared sample survived ( $\sim 3\%$ ).

**BAZZANIA TRILOBATA SURVIVAL UNDER CLEAR-CUT VS. INTACT FOREST CONDITIONS.** The second transplant experiment, initiated in July 2014, directly tested the survival of *B. trilobata* samples in a pair of clear-cut vs. intact *T. canadensis* forest plots. The intact forest plot included a typical density and basal area of trees for a Hemlock–Northern Hardwoods forest in the region (e.g., Bellemare *et al.* 2005), with basal area of 35.2 m<sup>2</sup>/ha overall, of which 51% was *T. canadensis* and 40.6% was *Betula lenta*. In contrast, the clear-cut forest plot had total basal area of only 4.3 m<sup>2</sup>/ha and this lesser amount was comprised of 93% deciduous *B. lenta* and no *T. canadensis*. Among the 20 samples of *B. trilobata* moved to the clear-cut plot in 2014, over half of the specimens ( $\sim 55\%$ ) declined and died by June 2017. In contrast, survival was significantly higher in the adjacent intact *T. canadensis* forest plot: 19 of 20 specimens remained intact over the 3-yr experiment (1 specimen lost to animal disturbance) and only 1 of these remaining 19 intact specimens declined and died (5.3%) over that time. This difference in

survival rates between the intact vs. clear-cut plots was significant (Pearson's  $\chi^2$  test with Yates' continuity correction:  $\chi^2 = 9.1007$ ,  $P = 0.0026$ ). Final size of *B. trilobata* samples paralleled trends in overall survival: Specimens in the intact forest plot averaged  $49.0\% \pm 7.0\%$  SE of their original size after 3 yr, while the surviving samples in the clear-cut plot averaged  $10.8\% \pm 5.7\%$  SE.

**Discussion.** The results of this experimental transplant study suggest that the liverwort *B. trilobata* is highly dependent on mature, intact *T. canadensis* forest habitats for its long-term survival and growth in our study area in central New England. When collected and replanted into our intact control site in a mature, *T. canadensis*-dominated forest, *B. trilobata* samples showed high survival (94%) and modest growth ( $65.4\% \pm 8.5\%$  SE of original size) over 4 years. In contrast, samples of *B. trilobata* experimentally transplanted into areas including sites with higher solar radiation, a higher density of young trees, and lower *T. canadensis* importance, survival and growth was substantially lower (e.g., 82% survival; mean size:  $34.7\% \pm 2.8\%$  SE). These trends were associated with significant effects of solar radiation, tree abundance, and *T. canadensis* importance on *B. trilobata* performance in our multiple linear regression results (Table 1).

Although the overall trend for the *B. trilobata* samples in this study was a decline relative to their initial size, surviving samples did show new growth and stem extension each season and most appeared to have reestablished on the forest floor. The exceedingly low growth rate of *B. trilobata*, even under ideal conditions (Cleavitt *et al.* 2007), suggests that our observations of survival and new growth over 4 years is likely indicative of longer-term trends toward establishment and eventual spread for a subset of the experimental samples. Most importantly, the results suggest that the unique understory environment of mature *T. canadensis* forests, typically including lower light levels and cooler conditions (Ellison *et al.* 2005), might be crucial to the growth and long-term survival of *B. trilobata*. Consistent with this interpretation, we saw dramatic declines and increased mortality when *B. trilobata* samples were experimentally moved in our second experiment into a recently clear-cut forest area compared to nearby intact *T. canadensis* forest. Likewise, even in the intact forest areas, deciduous leaf litter

removal proved to have a significant positive effect on performance, underscoring the apparent benefits for *B. trilobata* of growing under evergreen, small-needled *T. canadensis*. Overall, our results suggest the possibility of an important commensalistic relationship in which *B. trilobata* is positively influenced by the presence of *T. canadensis*, while also being negatively affected by deciduous tree species and severe canopy disturbance.

**ENVIRONMENTAL FACTORS AND *B. TRILOBATA* PERFORMANCE.** Based on the results of the multiple linear regression analysis (Table 1), all of the predictor variables quantified, except for soil organic layer moisture content, showed significant associations with the performance of transplanted *B. trilobata* samples. The strongest predictor of *B. trilobata* status was the average solar radiation each sample point received based on its slope and aspect ( $P = 0.0005$ ; Table 1). This strong relationship likely results from the variable thermal environment and associated desiccation risks created by increased solar radiation on south-facing vs. north-facing slopes at our experimental site. In particular, samples of *B. trilobata* performed better on the cool, north-facing slope than on the opposite, warmer south-facing slope. As a liverwort, *B. trilobata* lacks stomata and accomplishes gas exchange via relatively large, open air pores (Vanderpoorten and Goffinet 2009), potentially exposing it to significant desiccation risk when moved to warmer and drier conditions beyond its typical habitat niche. The high sensitivity of liverworts to changing forest conditions and disturbance has been noted elsewhere (Fenton *et al.* 2003, Åstrom *et al.* 2005). The finding that soil moisture conditions *per se* did not correlate with *B. trilobata* performance might be indicative of particular sensitivity of the liverwort to ground-level air temperature and moisture conditions, which regulate its internal water status, rather than substrate moisture levels, due to bryophytes' lack of vascularized roots to efficiently tap soil water (Vanderpoorten and Goffinet 2009).

We also found that *B. trilobata* performance was significantly related to two aspects of forest structure and species composition. Somewhat counterintuitively, the total number of trees surrounding each sample point exhibited a negative association with performance. However, the proportion of these trees that were *T. canadensis*

showed a significant positive association with *B. trilobata* performance. These trends reflect higher survival and success of *B. trilobata* at sample points under mature canopies of larger, but more widely spaced, trees (often *T. canadensis*), contrasted to points under younger canopies with a higher density of smaller trees (often deciduous species). These findings likely reflect the buffering and amelioration of incoming solar radiation and microclimate provided by a mature forest canopy, particularly one with a high proportion of dense, evergreen *T. canadensis* foliage. Because the number of sample points located in clear-cut conditions in this first part of the study was small relative to the overall design ( $\sim 9$  points of 85 total, or  $\sim 11\%$ ), the poor performance of *B. trilobata* samples observed in this subset of low-tree-density areas was partly obscured by the high performance of *B. trilobata* in mature *T. canadensis* forest areas with large, widely spaced trees (see Forest Management section below for further discussion of responses to clear-cut conditions).

The positive association between *T. canadensis* importance and *B. trilobata* performance likely emerges as a result of several direct and indirect effects of the conifer on the understory environment. First and foremost, *T. canadensis* likely modifies abiotic conditions in the forest understory to favor slow-growing, stress-tolerant plant species, including forest bryophytes such as *B. trilobata*. Even with increased access to water and nutrients, biomass accumulation and stem elongation in *B. trilobata* is still quite low, underscoring this species' conservative growth strategy (Cleavitt *et al.* 2007). Forests dominated by *T. canadensis* typically have lower light levels, cooler temperatures, and more stable moisture conditions, while nutrient cycling and availability may be limited, all factors selecting for stress-tolerant plant species (Ellison *et al.* 2005; Zuskwert *et al.* 2014). Second, *T. canadensis* appears to strongly influence the biotic environment that understory plants experience. Indeed, at high abundance, *T. canadensis* typically renders the forest understory less hospitable to more light- and nutrient-demanding plant species (Ellison *et al.* 2005, 2016). In this sense, *T. canadensis* might indirectly facilitate stress-tolerant, slow-growing bryophytes such as *B. trilobata* by limiting competitive effects from larger-statured, faster-growing vascular plant species in the ground layer. For example, dense shrub layers casting deep

shade at ground level have been linked to low bryophyte diversity (Cleavitt *et al.* 2008).

More strikingly in terms of biotic effects, we found that burial by deciduous leaf litter presented a significant stress on the *B. trilobata* samples, with those actively kept free of leaf litter being, on average, ~17% larger by the end of the 4-yr gradient transplant experiment. Many samples that were left uncleared of leaf litter accumulated thick layers of fallen deciduous leaf leaves, cutting off access to light and resulting in yellow or brown discoloration or decay of *B. trilobata* tissues. This suggests that, even on sites with otherwise suitable abiotic conditions for *B. trilobata* (e.g., cool, north-facing slopes), the liverwort might decline and disappear over time due to burial by deciduous leaf litter, if *T. canadensis* were to be replaced by deciduous tree species.

Interestingly, results of prior research suggest that the overall response of the bryophyte flora to *T. canadensis* decline might be mixed. Although some specialized taxa, such as *B. trilobata* investigated in this study, seem poised to decline, other species appear to show a positive response to increased light levels and nutrient availability in the forest understory. For example, in a longitudinal study between 1994 and 2006, Cleavitt *et al.* (2008) compared bryophyte communities between intact and, later, declining *T. canadensis* stands in the Delaware Water Gap National Recreation Area. They noted increased species richness of bryophytes and an expansion of nitrophilous species as the ecosystem changed, particularly on new elevated substrates like coarse woody debris from dead *T. canadensis*. However, the results of our study, mimicking a longer-term transition from *T. canadensis* dominance to broad-leaved deciduous tree dominance, suggest that a subset of forest bryophytes, like *B. trilobata*, could eventually suffer, particularly due increased leaf litter burial.

**FOREST MANAGEMENT AND *B. TRILOBATA*.** To better isolate the potential effects of common forest management practices on *B. trilobata*, it is necessary to consider the results of the second transplant experiment, which directly compared the survival of *B. trilobata* samples moved into an open area created by recent clear-cutting of a *T. canadensis* forest. In this experiment, we detected a highly significant negative effect of clear-cut conditions on *B. trilobata* survival, where the majority of specimens died within 3 yr (~55% mortality), while almost all the samples installed at

the same time in a nearby intact *T. canadensis* forest survived (1 of 19 intact samples died, ~5% mortality). Both plots in the second experiment were on level ground with intermediate solar radiation levels and, as such, the results showing a positive effect of an intact forest canopy with abundant *T. canadensis* likely derive from this evergreen tree species' ability to modify and ameliorate the forest understory environment, an effect that would be abruptly lost with canopy removal. The findings of the second experiment do require the caveat that the plots in the two habitat types were not replicated, although the multiple samples per plot and relatively wide spacing of samples within plots suggest some generality to the results, and the close matching of physiographic setting between the two plots should increase power to isolate effects of management. Notably, in the first transplant experiment along transects, we also observed high mortality in the subset of samples located on the edge of the clear-cut area (~56% mortality; five of nine samples died), in close agreement with the results of the second experiment.

Unlike the gradual environmental changes likely to be caused by natural, multi-year *T. canadensis* decline following attack by the exotic insects HWA and EHS, forest management practices intended to hasten transition of forest stands from *T. canadensis* to other tree species, and recover economic value of *T. canadensis* lumber, trigger more immediate and severe changes in the understory environment (Kizlinski *et al.* 2002, Lustenhouwer *et al.* 2012, Orwig *et al.* 2013). Indeed, the results of our clear-cut transplant experiment suggest the possibility of rapid negative effects on *B. trilobata* following the removal of *T. canadensis* and the opening of the forest canopy. Thus, it appears that the dramatic changes in understory microclimate following intensive logging, including drying and increased light and temperature levels (Lustenhouwer *et al.* 2012), could have immediate negative impacts on forest understory bryophytes such as *B. trilobata*. In contrast, we suspect that the gradual decline and incremental replacement of *T. canadensis* by deciduous tree species following HWA and EHS mortality would not expose the understory to such extreme changes and the decline of *B. trilobata* would instead be linked to more gradual desiccation or smothering by deciduous leaf litter.

REGIONAL THREAT TO *B. TRILOBATA* IN PERSPECTIVE. Importantly, our focus on the close association of *B. trilobata* with *T. canadensis* forests and the risks for decline and loss of the bryophyte does require some caveats. In particular, while *T. canadensis* is endemic to the eastern USA, *B. trilobata* is much more widely distributed around the Northern Hemisphere (Schuster 1969, Buczkowska *et al.* 2010). This biogeographic pattern, along with field observations of *B. trilobata* growing in association with other conifers in regions of the northern USA and Canada, underscores that the close association between *B. trilobata* and *T. canadensis* described in this study is not a globally exclusive, specialized relationship. Rather, it appears that within our study region *T. canadensis* often occupies sites that are also abiotically suitable for *B. trilobata* and, as discussed above, the tree species might additionally modify the abiotic conditions of these sites and adjacent areas, rendering them even more hospitable for *B. trilobata*. While we would predict a substantial decline in the distribution and abundance of *B. trilobata* if *T. canadensis* is eventually lost from our region, it is clear that *B. trilobata* would continue to survive elsewhere, beyond the range of *T. canadensis*. It is also likely that this unique liverwort species would persist in small areas of higher-elevation forest in our study region, where *B. trilobata* occurs under boreal-type conifers (*e.g.*, red spruce, *Picea rubens* Sargent), and in some unusual, spatially limited conifer-dominated habitats at lower elevations (*e.g.*, Atlantic white cedar swamps of *Chamaecyparis thuyoides* (L.) Britton, Sterns, & Poggenb along the coast of southern New England). However, it appears that the vast majority of potential *B. trilobata* habitat in the region is associated with *T. canadensis* forest, so the decline and loss of this distinctive conifer would likely have severe impacts on the distribution and abundance of *B. trilobata*.

**Conclusion.** In the face of imminent *T. canadensis* decline and the species' replacement by deciduous tree species, such as black birch (*Betula lenta*; Orwig and Foster 1998, Ellison *et al.* 2005), we predict that the distribution and abundance of *B. trilobata* will also decline in our study region. This dynamic would represent a striking example of an indirect negative effect of exotic invasive insect pests on a nontarget forest plant species, a dynamic that has not been

documented in this study system previously. Most strikingly, the indirect negative effects of exotic insect pests on *B. trilobata* are likely to occur via their role in undermining a commensalistic interaction (positive effects of *T. canadensis* on *B. trilobata*), while also exacerbating an amensalistic interaction (negative effects of deciduous tree species on *B. trilobata* via leaf litter burial). It will likely take many years for these interactions to unfold in natural ecosystems in our study region; however, our use of experimental transplants and a space-for-time substitution approach allows for well-grounded estimation of these future ecological dynamics. Although considerable research has focused on the direct negative effects of exotic invasives (Lockwood *et al.* 2013), the results of this study and others highlight the potential for invasive species to also indirectly disrupt mutualisms and commensalisms among native species, spreading their negative impacts much more broadly through ecological communities.

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